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封面图说: 在长白山麓低海拔地区的晚秋季节,成片的白桦林用无数根白色的树干、树枝烘托着林冠上跳动的金黄色叶片,共生的柞木树冠用更浓重的颜色显示了它的存在,整个山梁层林尽染,秋意浓浓。

彩图提供: 陈建伟教授 国家林业局 E-mail: cites.chenjw@163.com

庞秋颖, 陈思学, 于涛, 王洋, 阎秀峰. 盐胁迫对拟南芥和盐芥莲座叶芥子油苷含量的影响. 生态学报, 2011, 31(16): 4534-4541.
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盐胁迫对拟南芥和盐芥莲座叶芥子油苷含量的影响

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摘要: 芥子油苷是十字花科植物中一类含氮、含硫的次生代谢产物, 与其水解产物在植物防御功能中有重要意义且与环境因子关系密切。以模式植物拟南芥(*Arabidopsis thaliana*)和盐生模式植物盐芥(*Thellungiella halophila*)为研究对象, 系统地分析了盐胁迫下二者芥子油苷组成和含量的变化规律。拟南芥(生长4周)和盐芥(生长6周)叶片的芥子油苷组成在盐胁迫后没有改变。拟南芥的芥子油苷总量、脂肪族芥子油苷总量、吲哚族芥子油苷总量受盐胁迫的影响均不显著, 而盐芥的则随盐胁迫增强先减少、后增加并高于对照水平。拟南芥脂肪族的3MSOP、5MSOP和吲哚族的4OHI3M、4MOI3M随盐胁迫增强而含量降低, 而脂肪族的6MSOH、吲哚族的I3M以及盐芥脂肪族的3MSOP则随盐胁迫增强有含量增加的趋势。拟南芥脂肪族的8MSOO和吲哚族的1MOI3M, 盐芥脂肪族的3MTP、Allyl、10MSD和吲哚族的4MOI3M, 在盐胁迫下的含量变化与盐芥芥子油苷总量的变化趋势一致。

关键词: 拟南芥; 盐芥; 芥子油苷; 盐胁迫

Effects of salt stress on glucosinolate contents in *Arabidopsis thaliana* and *Thellungiella halophila* rosette leaves

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Abstract: Glucosinolates are a group of plant secondary metabolites comprising at least 120 anionic thioglucosides with well-defined structures. Found in many members of the order Capparales, including important crops (e.g., oilseed rape, broccoli and cabbage), glucosinolates and their degradation products play important roles in plant defense and interactions with the environment. In the past decades, the importance of these nitrogen- and sulfur-containing plant secondary metabolites has become apparent due to their function as cancer-prevention agents, crop-protection compounds, and biofumigants in agriculture. In addition, the presence of glucosinolates in the model plant, *Arabidopsis thaliana*, has stimulated vigorous research efforts into these interesting amino acid-derived products. Here we report glucosinolate profiles in *A. thaliana*, a glycophyte, and its close relative *Thellungiella halophila*, a halophyte, under different salt stress conditions. Exposure of *A. thaliana* seedlings to 5-day salt stress led to chlorosis in young leaves under 50 mmol/L and 150 mmol/L NaCl, the latter exhibited stronger chlorosis phenotype. In contrast, *T. halophila* did not display obvious chlorosis under these conditions. It was clearly more tolerant to salt stress than *A. thaliana*. We then measured tissue water content and relative electrolyte leakage. NaCl treatment caused a significant decrease in tissue water content in *A. thaliana*, whereas it only caused a slight reduction in *T. halophila*. Relative conductivity, an indicator of membrane damage, was

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used to indicate electrolyte leakage. After a 5-day salt treatment, relative conductivity increased in both *A. thaliana* and *T. halophila*. However, the increase in *A. thaliana* was much higher than that in *T. halophila*. The composition of glucosinolates was not varied in the rosette leaves of four-week-old *A. thaliana* and 6-week-old *T. halophila*, which were irrigated with 50 mmol/L and 150 mmol/L NaCl. The contents of total, aromatic and indole glucosinolates were not varied significantly either. However, the contents of total, aromatic and indole glucosinolates decreased after 50 mmol/L NaCl treatment and increased after 150 mmol/L NaCl treatment. Aliphatic glucosinolates 3MSOP, 5MSOP and indole glucosinolates 4OHI3M and 4MOI3M in *A. thaliana* decreased with increasing NaCl concentrations, while aliphatic glucosinolates 6MSOH, indole glucosinolates I3M in *A. thaliana* and aliphatic glucosinolates 3MSOP in *T. halophila* increased with increasing NaCl concentrations. The contents of 8MSOO and 1MOI3M in *A. thaliana*, 3MTP, Allyl, 10MSD and 4MOI3M in *T. halophila* displayed a similar pattern of variation. Interestingly, only two glucosinolates were identified to be common in both *A. thaliana* and *T. halophila*, but they exhibited significantly different patterns in response to salt stress.

Key Words: *Arabidopsis thaliana*; *Thellungiella halophila*; glucosinolates; salt stress

芥子油苷(glucosinolates, GS)又称硫代葡萄糖苷,是一类由氨基酸衍生的含氮、含硫的植物次生代谢产物^[1-2],主要分布于十字花科植物。根据氨基酸来源可以将芥子油苷分为脂肪族芥子油苷、芳香族芥子油苷和吲哚族芥子油苷3个类群,芥子油苷在植物与环境之间的相互作用中具有重要意义并引起人们极大的研究兴趣^[3-4]。植物的次生代谢是植物在长期进化过程中与环境相互作用的结果,芥子油苷代谢以及在体内的分布除了受自身基因的控制外,还受到植物生存环境(生物环境和非生物环境)的影响^[2,5-11]。尽管人们已经了解到非生物因子会影响植物体内芥子油苷含量,如季节、温度、光照、水分、硫营养对植物的生长产生各种各样的影响甚至胁迫,进而影响芥子油苷的代谢,但至今为止芥子油苷在植物响应非生物逆境中的作用还不清楚^[4, 12]。

盐胁迫是植物生长发育的主要限制因子之一,植物对盐胁迫的响应成为植物研究的一个重点和热点^[13-16]。根据植物对盐逆境的抗性反应程度,可以将植物分为盐生植物和淡土(甜土)植物或非盐生植物。拟南芥是现代植物生物学研究的模式植物,但由于拟南芥属于甜土植物,对盐胁迫比较敏感,一般认为它不适合用于耐盐性机理的研究。人们发现十字花科的盐芥(*Thellungiella halophila*)非常耐盐,能够在300 mmol/L NaCl的生境中完成生活史,而且与模式植物拟南芥的亲缘关系非常近^[17-18]。克隆的EST分析发现盐芥大约有95%的cDNA和氨基酸序列与拟南芥相同^[19],因此有研究者提出将盐芥作为研究耐盐性的模式植物^[17-18]。盐芥植株大小、形态和发育特征与拟南芥非常相似,全生育期与拟南芥类似,但生长较缓慢。目前,对盐芥研究主要集中在耐盐基因和生态生理方面,如盐胁迫条件下渗透调节^[20-21]、离子分布^[17]、质膜和液泡膜的SOS1及H⁺-ATPase活性变化^[22]、耐盐基因和基因转录水平调控^[23-25]、蛋白质组学研究^[26]等,并取得了大量研究成果。作为一种十字花科植物,盐芥体内芥子油苷种类、含量已有报道^[27],但对盐胁迫的响应尚未有报道。本研究以拟南芥、盐芥为实验材料,比较并分析盐胁迫条件下二者叶片中芥子油苷含量的动态变化过程。

1 材料和方法

1.1 植物材料培养及处理

实验所用拟南芥(*Arabidopsis thaliana*)为哥伦比亚生态型(ecotype Col-0),种子购自拟南芥生物资源中心(Arabidopsis Biological Resource Center, US),盐芥(*Thellungiella halophila*)为山东生态型,种子由山东师范大学张慧教授惠赠。

种子消毒冲洗后,置于4℃黑暗环境中打破休眠,播种在土和蛭石(1:1)的混合培养基中,人工气候室培养(8/16 h 光周期,25/20℃,光照150 μmol·m⁻²·s⁻¹,湿度50%—70%),每隔3d浇1次水。拟南芥生长至4周、盐芥生长至6周(植株大小与生长4周的拟南芥基本一致)时,分别用50、150 mmol/L NaCl溶液浇灌进行

盐胁迫处理,正常浇水的植株作为对照,连续处理5d后进行采样,样品直接用液氮冷冻,置于-80℃冰箱保存。每个处理至少3组重复。

1.2 组织含水量的测定

植物材料称单株鲜重后105℃杀青30 min,80℃烘至恒重后称干重。组织含水量为叶片水分占叶片鲜重的百分比:[(鲜重-干重)/鲜重]×100%

1.3 相对电导率的测定

相对电导率按照李合生等^[28]的方法测定:相对电导率=(处理电导率/煮沸后电导率)×100%

1.4 芥子油苷的测定

芥子油苷的提取、测定按照任欢等^[29]的方法。

2 结果与分析

2.1 盐胁迫对拟南芥、盐芥生长的影响

分析并比较盐胁迫条件下拟南芥和盐芥芥子油苷含量的动态变化过程,需要先了解二者生长受盐胁迫的影响及差异。生物量是体现植物生长状况的直接指标,组织含水量、表征膜透性的相对电导率则更能反映植物在盐胁迫下隐于表观形态之下的生理水平上的变化。

从植株的整体生长情况来看,随着盐浓度的增加,拟南芥的长势减弱。生长4周的拟南芥,正常浇水处理的对照组长势旺盛,50 mmol/L NaCl处理的植株部分幼嫩叶片已经发黄,150 mmol/L NaCl处理的植株大部分叶片褪绿,老叶出现不同程度的萎蔫。相比之下,盐芥的长势受盐胁迫影响不明显,150 mmol/L NaCl处理的植株只有部分幼嫩叶片叶色变浅,但植株长势良好。

测定的几项与生长相关的指标(图1)也证实了盐芥的抗盐能力优于拟南芥。伴随着生长受抑,拟南芥的叶片鲜重和干重均随盐浓度的增加而下降,而50 mmol/L NaCl处理的盐芥,单株叶片的鲜重和干重均大于对照植株,150 mmol/L NaCl处理的盐芥才低于对照植株。盐芥的叶片含水量随盐浓度的增加而下降,但下降幅度较小,50、150 mmol/L NaCl处理下含水量分别降低至85.36%、83.33%。相对电导率是反应质膜受损伤程度的常用生理指标。实验结果表明,50 mmol/L NaCl处理下拟南芥叶片的相对电导率(36.84%)比对照组(25.23%)略高,而150 mmol/L NaCl处理下的相对电导率则高达76.15%(图1),印证了150 mmol/L NaCl处理对拟南芥的严重伤害。盐芥在盐处理条件下相对电导率结果与拟南芥一致,但受影响程度整体低于拟南芥。NaCl胁迫5d后,对照组相对电导率为21.58%,50 mmol/L NaCl处理组相对电导率为28.90%,略高于对照组,150 mmol/L NaCl处理组相对电导率为62.78%,显著高于对照组。盐胁迫对盐芥质膜的伤害程度也是随着NaCl浓度的升高而逐渐增强。

2.2 盐胁迫对拟南芥芥子油苷含量的影响

在生长4周的拟南芥莲座叶中准确鉴定出9种芥子油苷(图2)。其中5种为脂肪族芥子油苷(aliphatic GS),包括3-甲基亚磺酰丙基芥子油苷(3-methyl-sulfinylpropylglucosinolate, 3MSOP)、4-甲基亚磺酰丁基芥子油苷(4-methylsulfinylbutylglucosinolate, 4MSOB)、5-甲基亚磺酰戊基芥子油苷(5-methylsulfinylpentylglucosinolate, 5MSOP)、6-甲基亚磺酰己基芥子油苷(6-methylsulfinylhexylglucosinolate, 6MSOH)和8-甲基亚磺酰辛基芥子油苷(8-methylsulfinyloctylglucosinolate, 8MSOO)。另外4种为吲哚族芥子油苷(indole GS),包括4-羟基吲哚基-3-甲基芥子油苷(4-hydroxy-indol-3-ylmethylglucosinolate, 4OHI3M)、吲哚基-3-甲基芥子油苷(indol-3-ylmethylglucosinolate, I3M)、4-甲氧吲哚基-3-甲基芥子油苷(4-methoxy-indol-3-ylmethylglucosinolate, 4MOI3M)和1-甲氧吲哚基-3-甲基芥子油苷(1-methoxy-indol-3-ylmethylglucosinolate, 1MOI3M)。

拟南芥莲座叶中脂肪族芥子油苷所占比例较大,占芥子油苷总量的75%左右,吲哚族芥子油苷所占比例较小。与其他芥子油苷相比,4MSOB含量较高。

NaCl处理后,拟南芥莲座叶芥子油苷的组成没有变化,各种芥子油苷所占比例的总体趋势也没有改变。各种芥子油苷含量的变化情况不同,从芥子油苷总量、脂肪族芥子油苷总量、吲哚族芥子油苷总量看,受盐胁

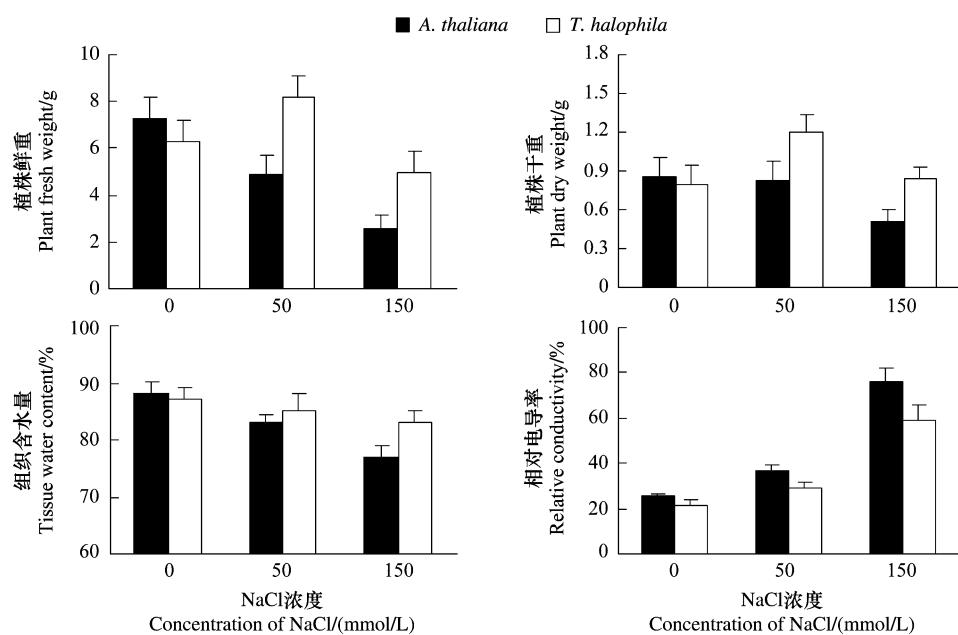


图1 盐胁迫对拟南芥、盐芥植株重量、组织含水量和叶片相对电导率的影响

Fig. 1 Effect of salt stress on *Arabidopsis thaliana* and *Thellungiella halophila* plant weight, tissue water content and relative conductivity

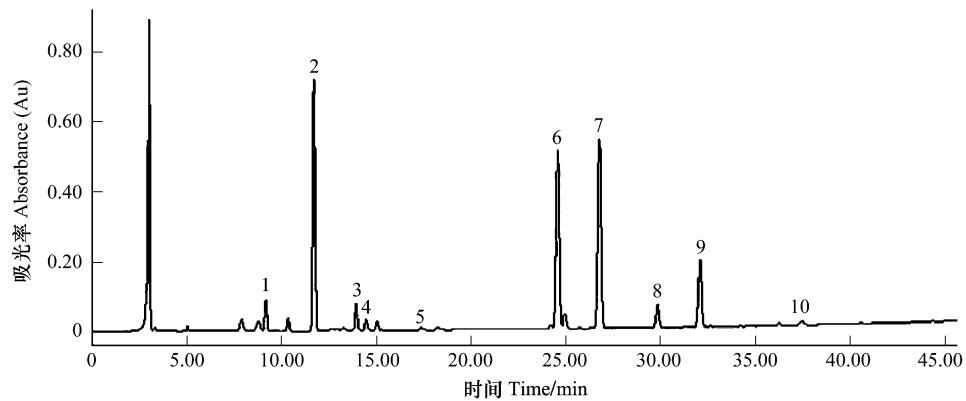


图2 拟南芥莲座叶芥子油苷的高效液相色谱图

Fig. 2 HPLC chromatogram of glucosinolates identified in rosette leaves of *Arabidopsis thaliana*

1. 3-甲基亚磺酰丙基芥子油苷 (3MSOP); 2. 4-甲基亚磺酰丁基芥子油苷 (4MSOB); 3. 5-甲基亚磺酰戊基芥子油苷 (5MSOP); 4. 6-甲基亚磺酰己基芥子油苷 (6MSOH); 5. 4-羟基吲哚基-3-甲基芥子油苷 (4OHI3M); 6. 苯甲基芥子油苷 (Benzyl; 内标); 7. 吲哚基-3-甲基芥子油苷 (I3M); 8. 8-甲基亚磺酰辛基芥子油苷 (8MSOO); 9. 4-甲氧吲哚基-3-甲基芥子油苷 (4MOI3M); 10. 1-甲氧吲哚基-3-甲基芥子油苷 (1MOI3M)

迫的影响均不显著(图3)。

含量变化较为明显的是脂肪族的3MSOP、5MSOP和吲哚族的4OHI3M、4MOI3M,它们均随着盐胁迫强度的增强而含量降低,而脂肪族的6MSOH、吲哚族的I3M则随着盐胁迫强度的增强有含量增加的趋势。脂肪族的8MSOO的变化趋势比较特殊,在50 mmol/L NaCl下含量略有下降,而在150 mmol/L NaCl下则恢复到近对照水平。另一变化规律比较特殊的是吲哚族的1MOI3M,50 mmol/L NaCl下含量略有降低,而在150 mmol/L NaCl下则显著高于对照水平1倍以上(图3)。

2.3 盐胁迫对盐芥芥子油苷含量的影响

在生长6周的盐芥莲座叶中准确鉴定出5种芥子油苷,其中4种为脂肪族芥子油苷,包括3-甲基亚磺酰丙基芥子油苷(3-methylsulphinylpropylglucosinolate, 3MSOP)、丙烯基芥子油苷(allylglucosinolate, Allyl)、3-甲硫丙基芥子油

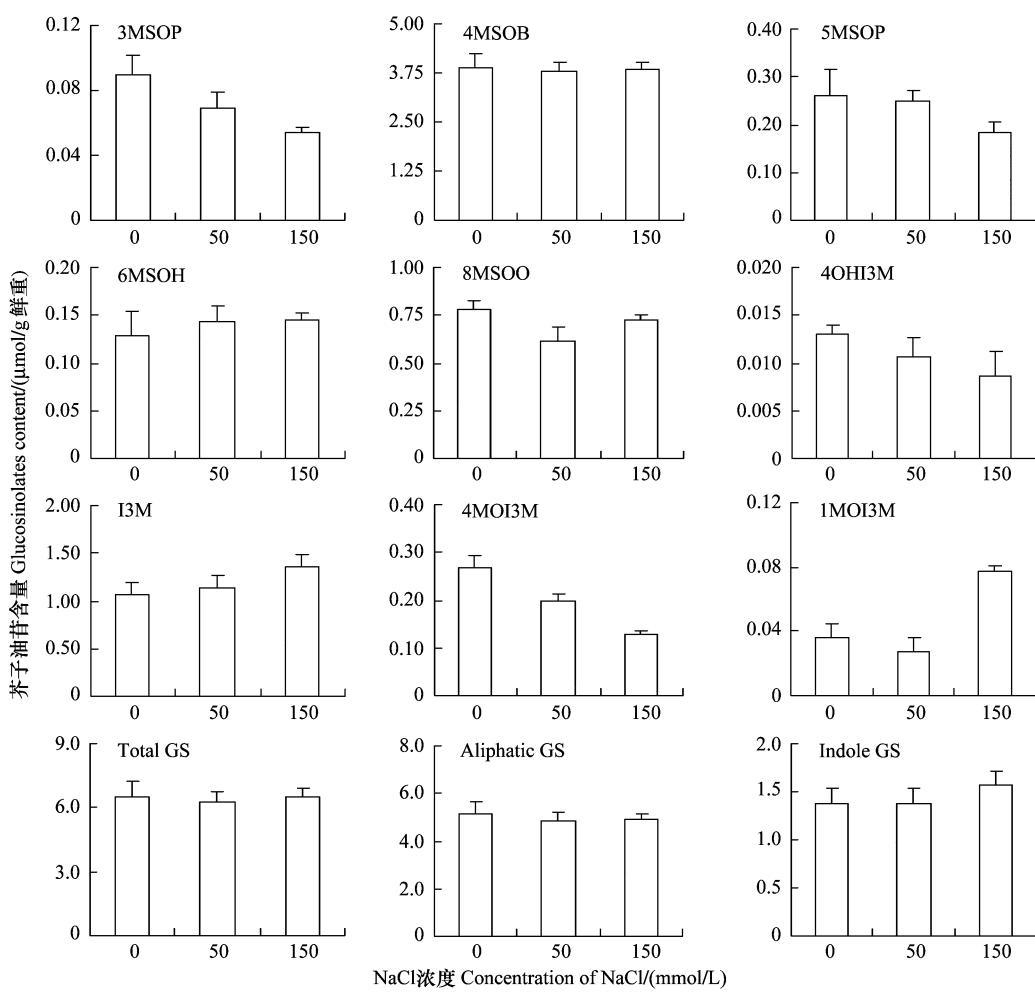


图3 NaCl处理拟南芥叶片芥子油苷含量的变化

Fig.3 Change of glucosinolate content in leaves of *Arabidopsis thaliana* during NaCl treatment

昔(3-methylthiopropylglucosinolate, 3MTP)、10-甲基亚磺酰癸基芥子油昔(10-methylsulfinyldecyglucosinolate, 10MSD), 只有1种吲哚族芥子油昔, 即4-甲氧基-3-吲哚甲基芥子油昔(4-methoxy-3-indolylmethylglucosinolate, 4MOI3M)。苯甲基芥子油昔(Benzylglucosinolate, Benzyl)为内标(图4)。

NaCl处理后, 盐芥莲座叶芥子油昔的组成没有变化, 仍为3MSOP、3MTP、Allyl、10MSD和4MOI3M。与其他芥子油昔相比, 盐芥莲座叶中3MTP含量较高。

盐胁迫下盐芥莲座叶的芥子油昔总量、脂肪族和吲哚族芥子油昔含量均有一定的变化(图5)。总芥子油昔含量与对照相比变化显著, 不同的NaCl浓度处理下变化趋势也不一致。50 mmol/L NaCl处理的总芥子油昔含量与对照相比大幅度下降(5.56 μmol/g鲜重), 仅为对照的55%。150 mmol/L NaCl处理的总芥子油昔含量则高于对照, 约为对照的1.23倍。

4种脂肪族芥子油昔中, 3MTP、Allyl和10MSD的变化规律与总芥子油昔基本一致, 而3MOP的含量呈现出随盐浓度增加而增加的趋势。唯一的一种吲哚族芥子油昔4MOI3M的变化规律也与总芥子油昔基本一致, 但在50 mmol/L NaCl处理下的下降幅度较小, 含量约为对照的89%。

3 讨论

芥子油昔是十字花科植物的重要次生代谢产物, 当温度、光照、水分、营养等环境条件发生改变, 或者植物受到昆虫取食、病原菌侵害、机械损伤时, 拟南芥、油菜和萝卜等植物会调节体内芥子油昔的含量来应答这些不良环境^[4,30]。目前有关盐胁迫对芥子油昔含量影响的研究较少。Qasim等^[31]对Dunkeld和Cyclon两种十

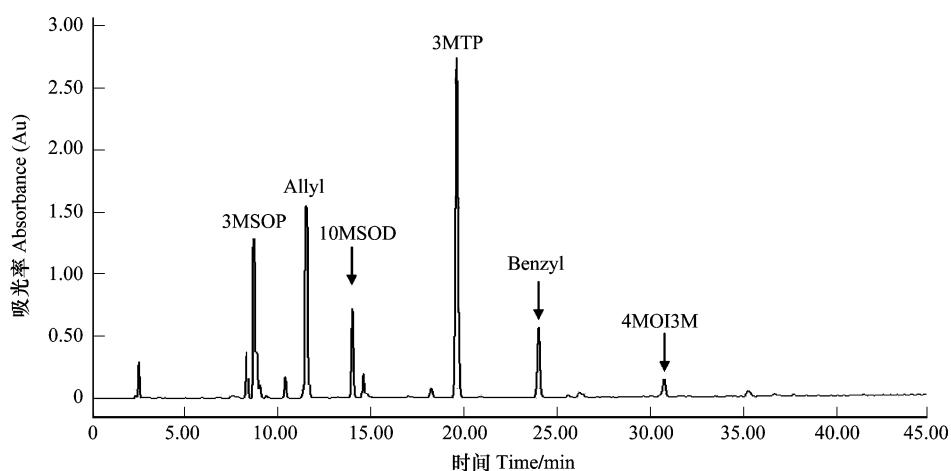


图 4 盐芥莲座叶芥子油苷的高效液相色谱图

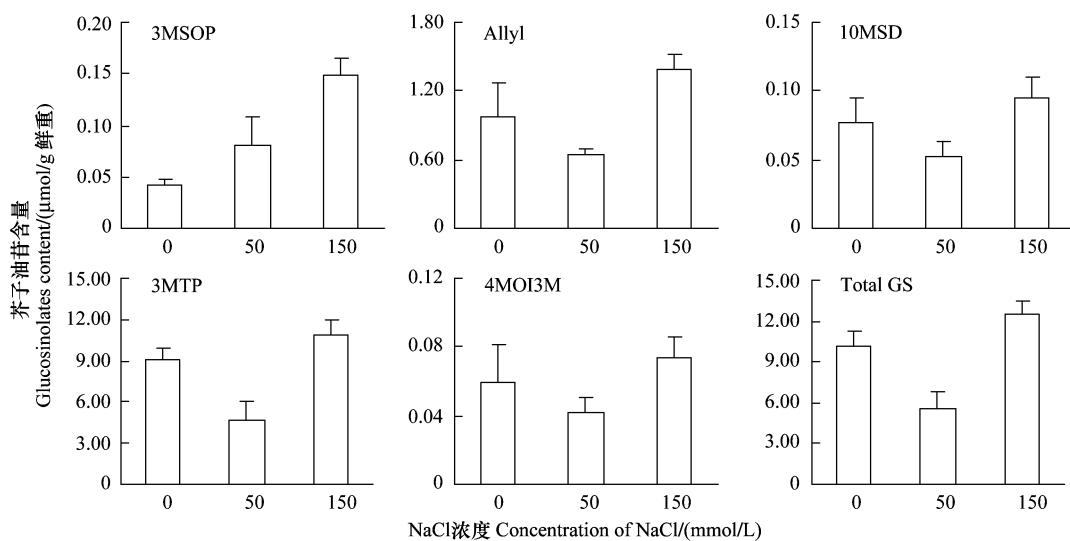
Fig. 4 HPLC chromatogram of glucosinolates identified in rosette leaves of *Thellungiella halophila*

图 5 NaCl 处理盐芥叶片芥子油苷含量变化

Fig. 5 Change of glucosinolate content in leaves of *Thellungiella halophila* during NaCl treatment

十字花科芸薹属(*Brassica*)的加拿大双低卡诺拉油菜进行盐胁迫,发现随着盐浓度增加,种子中芥子油苷含量逐渐升高。Ashraf 等^[32]对包括 Dunkeld 和 Cyclon 在内的 8 种芸薹属油料作物进行了盐胁迫处理,也发现种子中芥子油苷含量随着盐浓度增加逐渐升高,最多达到对照的 1.9 倍。López-Berenguer 等^[33]对花椰菜(*Brassica oleracea* var. *Ita'llica*)进行盐胁迫处理,发现叶片中芥子油苷受盐胁迫诱导含量升高。Yuan 等^[34]对萝卜(*Raphanus sativus*)幼苗进行 NaCl 胁迫,50 mmol/L 处理组总芥子油苷含量下降,但 100 mmol/L 处理组总芥子油苷含量升高。这些研究中,仅将总芥子油苷含量作为一项考察作物品质的辅助指标,并未深入分析芥子油苷组分在盐胁迫下的变化规律。

通过 NaCl 处理的方式对营养生长时期的拟南芥和盐芥进行盐胁迫处理,分析了盐胁迫下拟南芥莲座叶中芥子油苷含量的变化,发现芥子油苷总量、脂肪族芥子油苷总量、吲哚族芥子油苷总量受盐胁迫的影响均不显著。不过,进一步深入分析各个种类芥子油苷的变化细节发现,尽管盐胁迫后拟南芥莲座叶芥子油苷的组成没有改变,但各种芥子油苷含量在盐胁迫下的变化趋势并不一致。最近的研究表明,拟南芥受到机械损伤或干旱胁迫,叶片中各种芥子油苷的含量(芥子油苷的组合模式)也发生变化^[29,35]。由此可见,各种芥子油苷

占芥子油苷总量的比例受到非生物胁迫的影响,仅关注总芥子油苷总量在盐胁迫下的变化是不够的,不同种类的芥子油苷对盐逆境的响应以及可能担负的生理功能是有差异的。与拟南芥不同的是,NaCl 处理 5d 后,盐芥莲座叶的芥子油苷总量、脂肪族芥子油苷和吲哚族芥子油苷含量均发生了显著的变化。总体上,50 mmol/L NaCl 胁迫下芥子油苷的含量大幅度下降,而在 150 mmol/L NaCl 胁迫下芥子油苷含量又大幅度增加并超过对照水平,这与 Yuan 等^[34]对盐胁迫萝卜幼苗中芥子油苷的研究结果基本一致,低浓度的盐胁迫导致植物芥子油苷含量降低,高浓度的盐胁迫诱导芥子油苷含量升高。结合盐胁迫对盐芥生长影响的分析发现,伴随着高浓度盐胁迫下盐芥生长和初生代谢受抑,次生代谢产物芥子油苷的含量升高。有研究推测芥子油苷可能作为一种渗透调节物质在植物响应盐胁迫过程中提高植物的渗透调节能力^[12],那么在盐芥中芥子油苷是否具此功能以及通过何种方式参与渗透调节,有待进一步探讨。

在盐芥和拟南芥的莲座叶中,只有 2 种芥子油苷是共同含有的,即脂肪族的 3MSOP 和吲哚族的 4MOI3M。不过,3MSOP 含量对盐胁迫的响应在盐芥和拟南芥中却是截然相反的,盐芥的 3MSOP 含量随盐胁迫强度的增强而大幅度增加,而拟南芥的 3MSOP 含量则随盐胁迫强度的增强而迅速减少。4MOI3M 对盐胁迫的响应也不一样,盐芥中是随盐胁迫强度的增强而先减少后增加,而拟南芥中如同 3MSOP 一样随盐胁迫强度的增强而迅速减少。由此可见,盐生植物盐芥与甜土植物拟南芥在应对盐胁迫的过程中,次生代谢的响应也是不同的。

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3	植物生态学报	4384	3	应用生态学报	1.733
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6	植物生理学通讯	3362	6	西北植物学报	0.986
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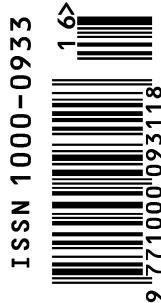
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